An Arctic Kelp Community in the Alaskan Beaufort Sea

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ABSTRACT.   The discovery of the "Boulder Patch", an area of cobbles and boulders with attached kelp and invertebrate life, is reported from Stefansson Sound, near Prudhoe Bay, Alaska. Geophysical surveys using side-scan sonar and low-frequency recording fathometers reveal that cobbles and boulders occur in patches of various sizes and densities. Despite a seasonal influx of sediments, the Boulder Patch is a nondepositional environment. Physical disruption of cobbles and boulders by deep draft ice is minimal due to offshore islands and shoals which restrict the passage of large ice floes into Stefansson Sound. The apparent absence of similar concentrations of rocks with attached biota along the Alaskan Beaufort Sea coast is explained by the scarcity of rocks in areas protected from ice abrasion and with no net sediment deposition. In Stefansson Sound, the rocks provide a substratum for a diverse assortment of invertebrates and several species of algae.

Recolonization by the biota was minimal on twelve boulders denuded and then left undisturbed for a three-year period. Sedimentation and grazing activity appear to be the major factors inhibiting recolonization. Linear growth in the kelp, *Laminaria solidungula*, is greatest in winter and early spring when nutrients are available for new tissue growth. The plant draws on stored food reserves to complete over 90% of its annual linear growth during the nine months of darkness under a turbid ice canopy. These reserves are accumulated by photosynthetic activity during the preceding summer. The total carbon contribution made by kelp in Stefansson Sound under these conditions is about 146 x 10^6 g·yr^{-1} or 7 g·m^{-2}·yr^{-1}. A small percentage of this carbon is consumed directly by herbivores, but its importance to other organisms is not known and is under investigation.

Key words: kelp, *Laminaria solidungula*, Flaxman boulders, Beaufort Sea, Boulder Patch, productivity, recolonization, geophysical surveys, side-scan sonar, lag deposits

RÉSUMÉ.   L'article rapporte la découverte d'un terrain couvert de grosses pierres et de galets sur lesquels vivent du varch et des invertébrés, au détroit de Stefansson, près de la baie Prudhoe, en Alaska. Des levées géophysiques de ce terrain nommé "Boulder Patch", effectuées à l'aide de sonars à balayage latéral et de fathomètres à basse fréquence, ont indiqué que les grosses pierres et les galets sont groupés en ensembles de diverses dimensions et densités. Même à l'augmentation saisonnière de sédiments, il n'y avait aucune accumulation de ces sédiments sur le terrain en question. Le dérangement physique des pierres et galets par les glaces profondes est minime grâce aux îles marines et aux hauts-fonds qui restreignent le passage de gros icebergs dans le détroit de Stefansson. L'absence apparente de concentrations semblables de roches sur lesquelles croît une biote, sur la côte de l'Alaska du côté de la mer de Beaufort, s'explique par la pénurie de roches dans les régions protégées de l'érosion par les glaces et ne recevant aucun dépôt. Dans le détroit de Stefansson, les roches servent de substrat à un éventail diversifié d'invertébrés et à un bon nombre d'espèces d'algues.

Il y eut peu de recolonisation par la biote sur douze grosses pierres dénudées et non dérangées pendant trois ans. La sédimentation et le pâturage semblent être les facteurs principaux empêchant la recolonisation. La croissance linéaire du varech, *Laminaria solidungula*, est plus prononcée au cours de l'hiver et au début du printemps, lorsque la présence des éléments nutritifs permet une nouvelle croissance des tissus. La plante se nourrit de ses réserves afin de compléter plus de 90% de sa croissance linéaire annuelle au cours de neuf mois de noirceur passés sous une épaisse couverture de glace. Ces réserves auront été accumulées par photosynthèse lors de l'été précédent. La distribution totale de carbone par le varech dans ces conditions, au détroit de Stefansson, est d'environ 146 x 10^6 g·année^{-1} ou 7 g·m^{-2}·année^1. Un léger pourcentage de ce carbone est consommé directement par les herbivores, mais son importance par rapport à d'autres organismes est inconnu et est en train d'être étudié.

Mots clés: varech, *Laminaria solidungula*, grosses pierres Flaxman, mer de Beaufort, Boulder Patch, productivité, recolonisation, levées géophysiques, sonar à balayage latéral, accumulations de pierres par déflation

Traduit pour le journal par Maurice Guibord.

РЕЗЮМЕ.   Арнтичнское Сообщество Бурой Водоросли в Море Бофорта на Аляске. Открытие "Места Валунов", область где бурая водоросль и беспозвоночные прикрепленные н булыжникам и валунам. Место Валунов находится в заливе Стефансона, близно залива Прудо, на Аляске. Геофизические обозрения сдепаны бокооглядыванным сонаром и эхолотом низкой частоты показывают что булыжники и валуны встречаются в группах различных размеров и густоты. Несмотря на сезон-ный приток осадоков, Место Валунов-неосадочное окружение. Физическое перемещение булыжников и валунов ледяными ниля минимальное потому что острова и носы ограничивают проход больших ледяных полей в заливе Стефансона. Явное

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отсутствие похожих концентраций скал с привязанными морскими организмами

вдоль берега моря Бофорта на Аляске объясняется недостатком скалов в местах

охраненных от ледяной абразии и без осадконакопления. В заливе Стефонсона,

скалы действуют основанием для разнообразных беспозвоночных и нескольких видов

морских водорослей. Колонизация этим организмам была минимальная на двенадцати

обнаженных валунах, которые три года не трогали. Осадконакопление и пасущиеся

животные казались важнейшими факторами препятствующими переколонизацию.

Линейный рост бурой водоросли, *Laminaria solidungula*, крупнее зимой, и рано

весной когда питательные вещества доступны новому росту ткани. Водоросль

употребляет углеводы, запасаны в лопасти, что бы выполнять больше 90% его

ежегодного линейного роста в течение девяти месяцев в темноте под мутном

ледяном потолком. Эти углеводы накопляются фотосинтезом в течение прежнего

лета. Общая продукция углерода бурыми водорослями в заливе Стефансона

приблизительно 146 x 10^6 г год$^{-1}$ или 7 г м$^{-2}$ год$^{-1}$. Небольшой процент этого

углерода пользуется травояуными животними, но важность этого углерода для других

организмов не известна и сейчас исследуется.

Russian abstract supplied by authors.

INTRODUCTION

A distinctive feature of the Alaskan Beaufort Sea shelf biota is the absence of kelp and other species of benthic macroalgae. Pieces of kelp and red algae have been found only as drift on beaches between Pt. Barrow and the United States-Canadian border, and entire plants are seldom observed in significant numbers in driftlines. Collins (1927), in the last major account of benthic algae of the Alaskan Beaufort Sea, indicated that no extensive stands of laminarioids were found between Pt. Barrow and the Mackenzie River, N.W.T. In contrast, many species of sublittoral benthic algae grow in the Canadian Arctic (Lee, 1973; Wilce, 1964).

The ecology of arctic kelp communities has not been studied, mainly because of the large amount of logistic support needed for a diving operation in the Arctic. Therefore, we know little about the energetic contribution made by sublittoral benthic algal communities to the arctic nearshore environment and the fauna associated with large stands of macroalgae. Lee (1973) postulated that colonization of submerged rocks in the Canadian Arctic by fast-growing ephemeral plants takes place after they are no longer icebound, but this hypothesis has not been tested. In temperate regions, subtidal field studies have addressed the temporal and spatial aspects of recolonization, the interaction among organisms, the importance of physical parameters, and the productivity of the algae in respect to its carbon or energetic input (Foster, 1975; Hatcher *et al.*, 1977; Vadas, 1977).

In August 1971, one of us (E.R.) discovered abundant kelp and a diverse invertebrate fauna attached to cobbles and boulders near Prudhoe Bay in Stefansson Sound, Alaska, in an area now designated the "Boulder Patch" (by the U.S. Board of Geographic Names). The Boulder Patch has been the subject of cooperative geological and biological studies since 1978. These studies resulted from the need to provide adequate protection to sensitive biologically-productive regions, while allowing simultaneous exploration of oil reserves in the immediate area. The Boulder Patch lies on top of promising offshore oil reserves, as indicated by the fact that some tracts in this area received the highest bids in the joint State-Federal Beaufort Sea lease sale in December 1979 (Wilson, 1979).

The Boulder Patch is a rare feature of the Alaskan Beaufort Sea shelf, which is blanketed predominantly by silty sands and mud (Barnes and Reimnitz, 1974). Most macroalgae depend on hard rock substrates for attachment, since they require a stable base for successful colonization, growth and reproduction. This fundamental need for a hard substratum was recognized by Kjellman (1883), in his classic treatise on arctic algae.

Mohr *et al.* (1957) first reported the existence of a kelp bed in arctic Alaskan waters. Using a dredge, they collected a large amount of seaweeds, fishes and invertebrates at 13 m depth about 50 miles southwest of Pt. Barrow

in the Chukchi Sea. Collection of algae elsewhere in the Alaskan Arctic has been limited to drift material picked up by various Canadian and American arctic expeditions during the late 19th and early 20th centuries (for complete review, see Mohr et al., 1957).

This paper combines marine biological and geological studies to: (a) delineate the areal extent and configuration of the Boulder Patch; (b) explain the reasons for the existence of the unique geologic setting; (c) document seasonal variations in the physical environment that affect the development of the biotic community; and (d) describe the composition of the community and determine the productivity of the kelp. Repeated monitoring of a study site allowed detailed description of ecological and biological processes in light of seasonal variations in the environment. Such information is valuable in evaluating the importance

of kelp communities and their probability of occurrence on arctic shelves. The locations of other known and suspected occurrences of algal beds in the Alaskan Beaufort Sea are presented.

STUDY AREA

Description of Stefansson Sound

Stefansson Sound extends from the Midway Islands in the west to Tigvariak Island in the east, and is enclosed by the protecting barrier island chain that consists of the McClure Islands, Dinkum Sands, Cross Island, and the Midway Islands (Fig. 1). Water depths in Stefansson Sound do not exceed 10 m, and range from 3 to 9 m within the Boulder Patch. Waves have a short period because of shallow depth and limited fetch. Even during storms, waves
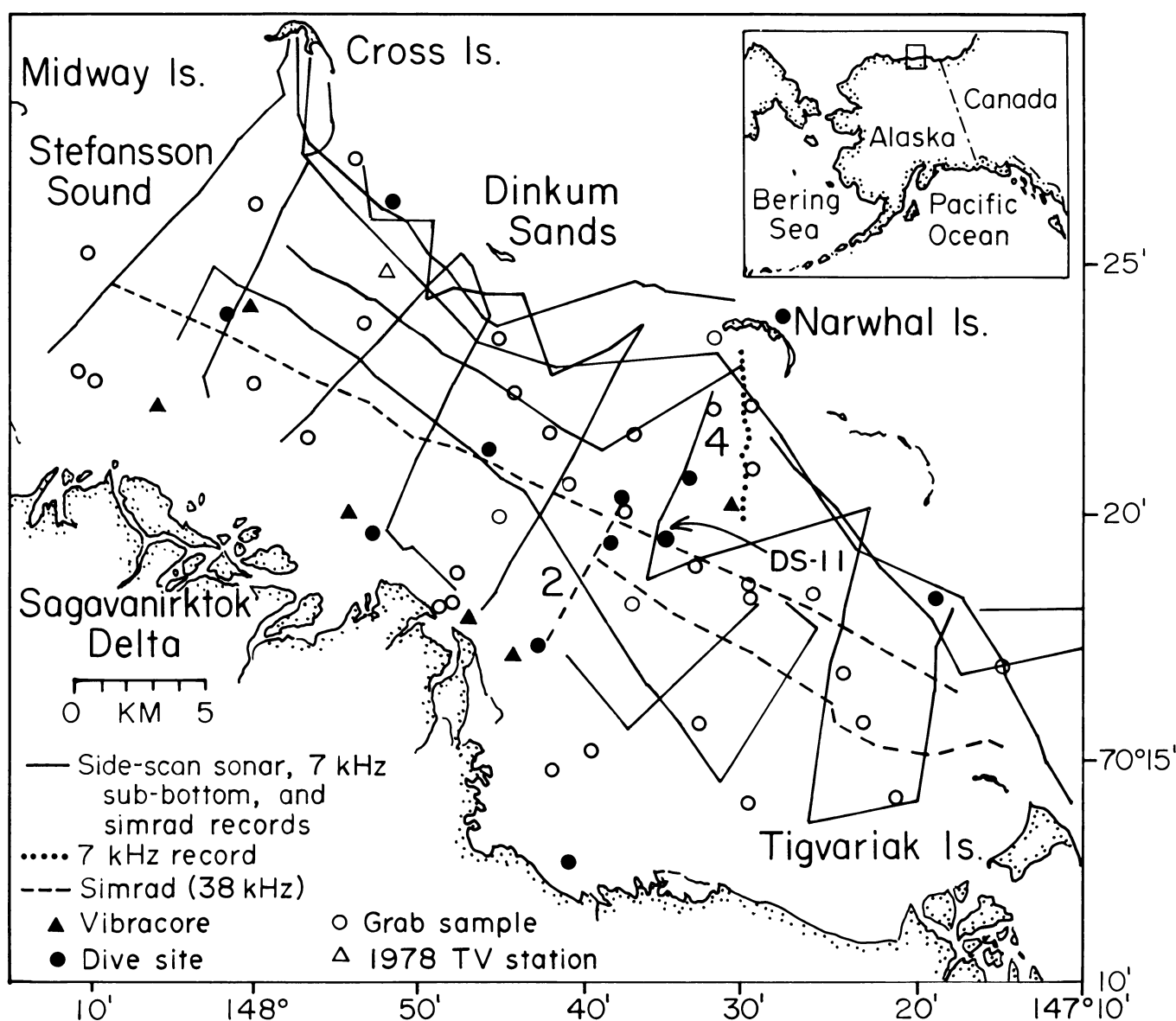

FIG. 1.   The location of Stefansson Sound Dive Site 11 (DS-11), survey tracks and sampling sites pertinent to the Boulder Patch study area. The location of Figures 2 and 4 are shown by large numbers.

rarely exceed 1.5 m. Currents are predominantly wind-driven during the open-water period, when easterly winds dominate. Therefore, the net drift is westward during the summer (Barnes *et al.*, 1977; Matthews, 1981a). The rivers discharging into the sound supply only sand-size and finer materials. Peak discharge occurs in June following the river breakup, but very little sediment accumulates within the sound (Reimnitz and Ross, 1979). Currents are very weak to undetectable during the period of total ice cover (from mid-October through June). Bottom water temperatures in the vicinity of the Boulder Patch range from a nearly constant $-1.9°C$ under the sea ice to $7°C$ during the open-water period. Salinity varies from 14 to 35‰ (Barnes *et al.*, 1977). With the exception of the Boulder Patch, the bottom is characterized by silty sands and mud, and an infaunal assemblage dominated by polychaete worms, small molluscs and crustaceans (Feder and Schamel, 1976; Broad *et al.*, 1978).

Freeze-up is usually complete by mid-October, and breakup begins in late June or early July. The benthic environment is largely protected by the offshore islands and shoals from gouging by deep draft ice. The winter ice field within Stefansson Sound is shorefast (i.e., attached to the shore), with minimal movement from early November through June. Ice thickness reaches a maximum of 2 m in early May before deterioration of the ice canopy begins.

MATERIALS AND METHODS

Field Logistics

During the open-water period, we sampled from two boats. The 13-m R.V. *Karluk* (U.S. Geological Survey) was used in geophysical work, sampling, and diving. A 6-m Boston Whaler (the R.V. *Arctic Char;* National Oceanic and Atmospheric Administration) was used for biological studies that employed divers. In the winter, we did most of the diving at an acoustically marked study site, Dive Site 11 (DS-11; 70°19.25'N,147°35.1'W; Fig. 1). During ice-covered periods divers entered the water through holes cut in the ice with augers and ice chisels. Ice blocks were removed by helicopter or multiterrain vehicle (Rolligon). A heated, insulated hut (Parcoll, Panebec Ltd., Montreal) placed over the dive hold functioned as a dive shelter and laboratory. Each diver wore a dry suit, a primary and backup breathing system, and headphones for wireless underwater communication with the surface (UDI-SUBCOM, Aberdeen, Scotland). Liquid silicone injected into the barrel of the first stage of the regulator prevented freeze-ups in the breathing system, especially when we dove without a shelter. Divers were tethered to the surface and were usually limited to a 25-m radius of the hole, although we occasionally ventured up to 50 m distant for short periods under special circumstances.

The Physical and Chemical Environment

We used several types of survey equipment to delineate the distribution of cobbles and boulders on the seabed.

This equipment included side-scanning sonar, the Raytheon RTT-1000 system with both a 200 kHz narrow beam transducer for bathymetry and a 7 kHz transducer for sub-bottom information, and a Simrad "Partner Sounder" operating at 38 kHz. A Del Norte Trisponder system was used for navigation, and the fixes were accurate to within ±5 m. Additional data, including surface samples, vibracores, and diving observations were collected at numerous sites. Sample locations, survey tracks and the types of survey equipment used along the various traverses are shown in Figure 1.

At DS-11, divers observed the accumulation of sediments over a two-year period. Here sediment settled upon biota and boulders, and on large plastic trays anchored in place. Measurements of the sediment cover were made with a ruler to the nearest 0.5 mm when the accumulation was greater than 0.5 mm. Sediments were collected for analysis in a large plastic cylinder, approximately 150 cm in diameter and 50 cm high, suspended 1 m above the seafloor. This sediment collector was deployed for a period of four months, from late May to late August 1981. The textural analysis of the trapped sediment used the methods of Folk (1974). Percent organic composition was calculated by loss on ignition at 550°C for two hours.

Inorganic nitrogen (nitrate and nitrite) was measured in water samples collected 1-3 m off the bottom near DS-11. Nitrate and nitrite were determined according to Strickland and Parsons (1972).

Photon flux density was measured with an LI-185 quantum radiometer/photometer with an LI-192S underwater quantum sensor (LI-COR, Inc., Lincoln, Nebraska).

The Biological Community

Biological sampling and *in situ* experiments were conducted by a team of divers at approximately three-month intervals between July 1978 and November 1981, at DS-11 (Fig. 1). During the open-water period, samples were collected at DS-11 and at several other locations in the Boulder Patch. Fauna were preserved in formalin and bottled in the field. Macroalgae were mounted on herbarium paper or preserved in formalin.

Species composition and biomass of epilithic organisms were determined by scraping and airlifting all biota within 50 replicate 0.05 m^2 areas on rock surfaces. Samples were taken haphazardly but rocks with attached brown algae were avoided because of the difficulty of sucking these large plants into the airlift without breaking them into many pieces. This also allowed efficient collection of the epilithic biota without clogging the airlift intake with large pieces of *Laminaria*. The material from each scrape was sorted, identified, enumerated and weighed in the laboratory. Biomass and density of the biota are expressed per m^2 of rock substrata, not per m^2 of seabed (rock cover at DS-11 is estimated at 42%).

Brown algal standing crop was estimated by collecting all attached plants within twenty-five 0.25-m^2 areas along 50-m transect lines. Ten transects were examined in areas

where rock cover exceeded 25%, and 10 were examined in areas where rock cover ranged between 10 and 25%. These areas were defined by recent industry-sponsored geophysical surveys of the Boulder Patch (Toimil, 1980).

Recolonization

Recolonization of 0.05-m^2 plots denuded with paint scrapers and wire brushes was observed and photographed during each visit to DS-11. Two to four plots were denuded at approximately three-month intervals beginning in August 1978 and ending in May 1979, for a total of 14 plots. Composition, density and percent cover of the colonizing organisms were determined from both photographs and *in situ* analysis of the plots. Only the central 100-cm^2 area was analyzed to reduce edge effects. All plots were located on level surfaces on boulders.

Primary Production

Linear growth of *Laminaria solidungula*, the predominant kelp, was followed by punching holes in the base of the blade, above the meristematic region (Chapman and Craigie, 1977). Production-to-biomass ratios were calculated to determine the total carbon input made by the brown algae to the marine environment. Since *L. solidungula* constitutes over 90% of the brown algal biomass, we focused on the productivity of this plant. The blade of *L. solidungula* is divided into distinct ovate segments of different sizes by constrictions that form annually. The growth of a new basal blade segment starts in November and continues until the following November. Since attrition occurs at the distal portion of the blade, the biomass of the basal segment is an accurate measurement of the plant's annual production. Seventeen plants, weighing between 1.5 and 33 grams, were carefully detached from their substratum in November 1979, and banded to a large plastic Vexar

cage anchored to the seafloor for one year. Following retrieval of the cage in November 1980, the new basal segments of the plants were individually removed and weighed. These wet weights represented the annual production of the plant. The average annual production-to-biomass (P:B) ratio was obtained by dividing the biomass of the first blade segment by the initial plant weight. The percentage of dry weight to wet weight was determined by drying algal tissue in an oven at 30°C for 48 hours. The plants used for wet-weight-to-dry-weight determinations were collected haphazardly by divers at DS-11.

Taxonomy

The taxonomic literature available on the organisms collected in this community is remarkably complete except for two groups, Anthozoa (sea anenomes), and Opisthobranchia (nudibranchs). This is due, in part, to the thorough collections made on several Canadian and American expeditions during the late 1800s and early 1900s, and by early arctic explorers such as Kjellman (1883). The Russians also have made a substantial contribution to our taxonomic knowledge of arctic biota. We used over 70 references to identify the flora and fauna and were fortunate to have the cooperation of several specialists who are listed in the acknowledgements. Dunton and Schonberg (1979) provide a complete list of the references used to identify the organisms collected in the Boulder Patch.

RESULTS

Geological Features of Stefansson Sound

The Simrad depth sounder proved to be the most reliable trackline survey tool for delineating the distribution of cobbles and boulders (Fig. 2). Bottom traces in the area of the Boulder Patch are characterized by elongated return
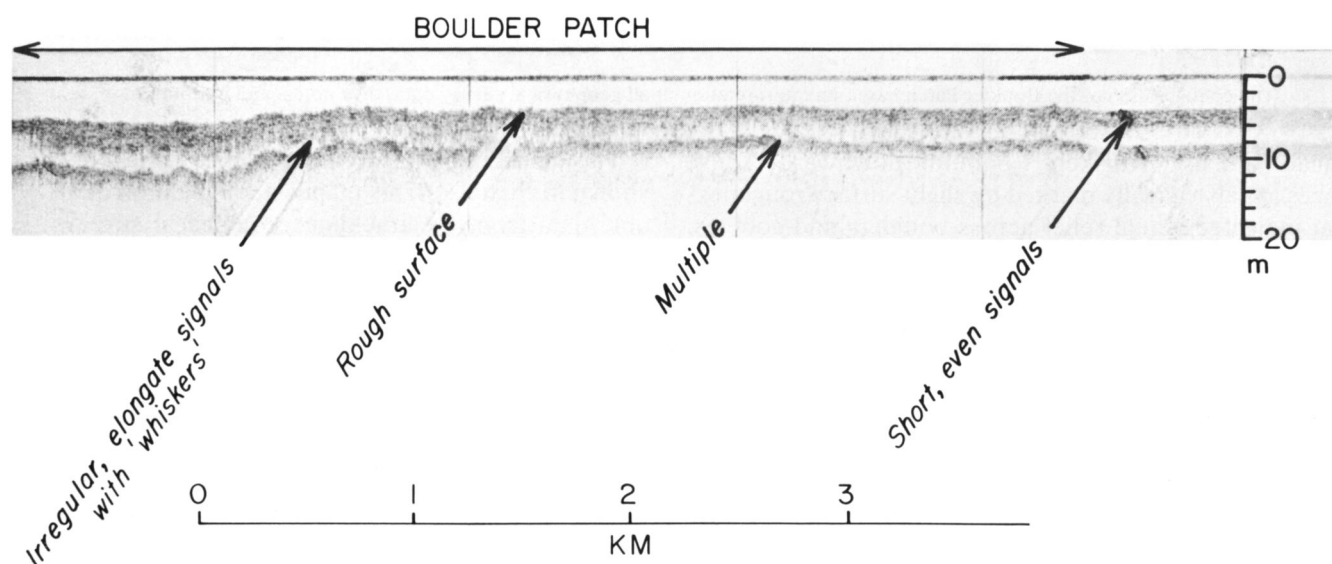

FIG. 2.   The Simrad 38 kHz depth recorder trace of a boulder patch is characterized by irregularly elongated signals and by slight surface roughness. For the location of this record see Figure 1.
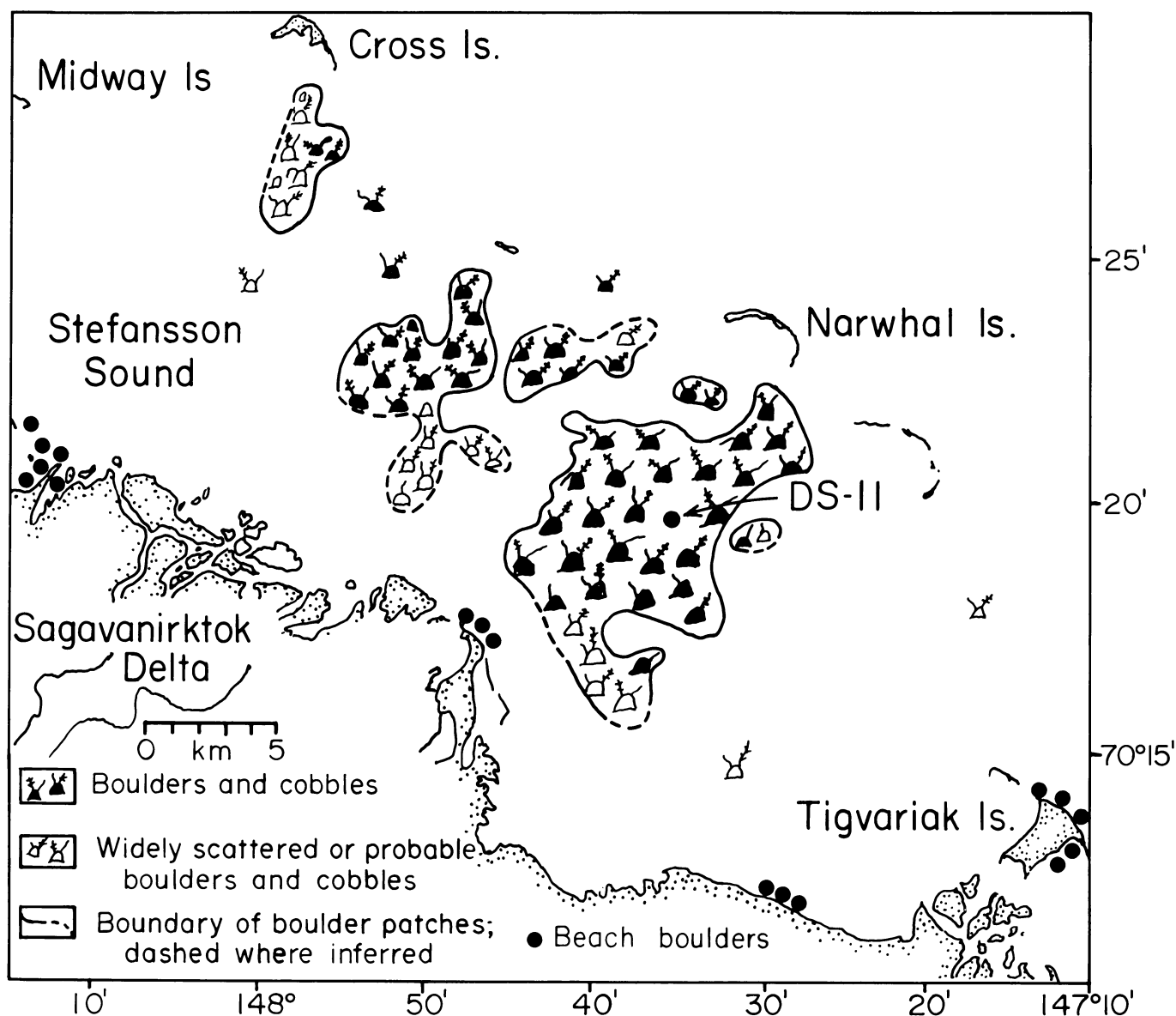
FIG. 3.   The configuration of the Boulder Patch based on interpretation of all geophysical survey data, dive notes, and bottom samples.

signals and by "whiskers" pointing downward. These traces are also usually marked by slight surface roughness that indicated actual relief across boulders and cobbles. The reliability of these criteria for recognizing the boulders or cobbles was verified by four dives.

In some areas the side-scan sonar did not support the Simrad trace, possibly because of poor resolution caused by abundant marine growth, which tends to diffuse high frequency signals (Reimnitz and Ross, 1979). Nonetheless, the side-scanning sonar was useful in providing supporting data over a large extent of the trackline. The Raytheon RTT-1000 traces, obtained with a narrow-beam 200 kHz transducer, showed rough relief within the Boulder Patch with individual spikes indicating single boulders. However, these traces were only clear on calm days. The Raytheon 7 kHz records were not useful for locating cobbles or boulders.

The distribution of areas of cobbles and boulders is shown in Figure 3. This map is a compilation of all available data from the trackline geophysical surveys, supported by benthic samples and diving traverses. The rocks are not distributed uniformly but in patches of various sizes. Figure 3 shows clearly identifiable areas of dense rock bottom, and transition areas where finer sediments dominate, or where our data are uncertain. Subsequent geophysical studies in portions of Stefansson Sound (Toimil, 1980) generally agree with the distribution mapped here.

Seismic sub-bottom reflection traces (7 kHz) in portions of the Boulder Patch indicate that the boulders on the shelf surface are located in areas where Holocene marine sediments are thin or absent. Figure 4 shows our interpretation of a typical seismic reflection record extending from Narwhal Island on the left southeastward toward the Saga-
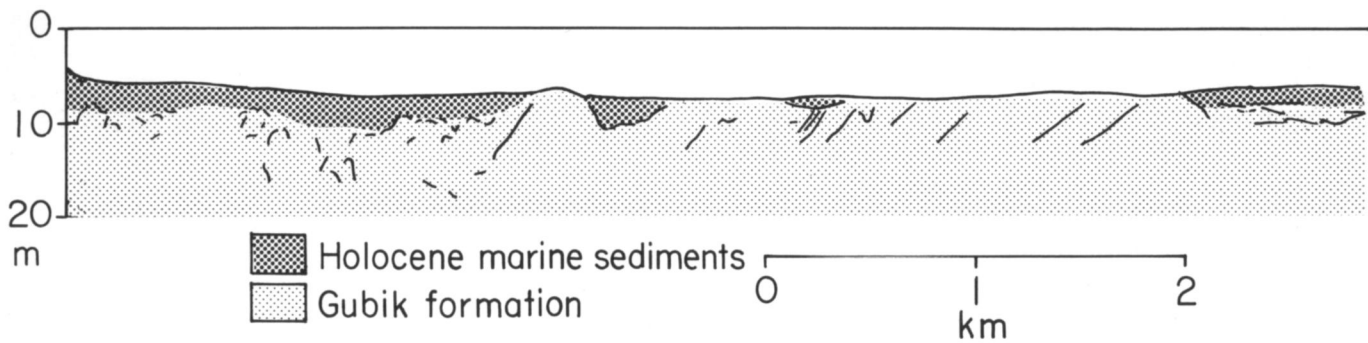
FIG. 4.   Line drawing of a 7 kHz seismic sub-bottom record across part of the Boulder Patch, showing the underlying Gubik exposed and truncated by the sea floor. For location of this cross-section see Figure 1.
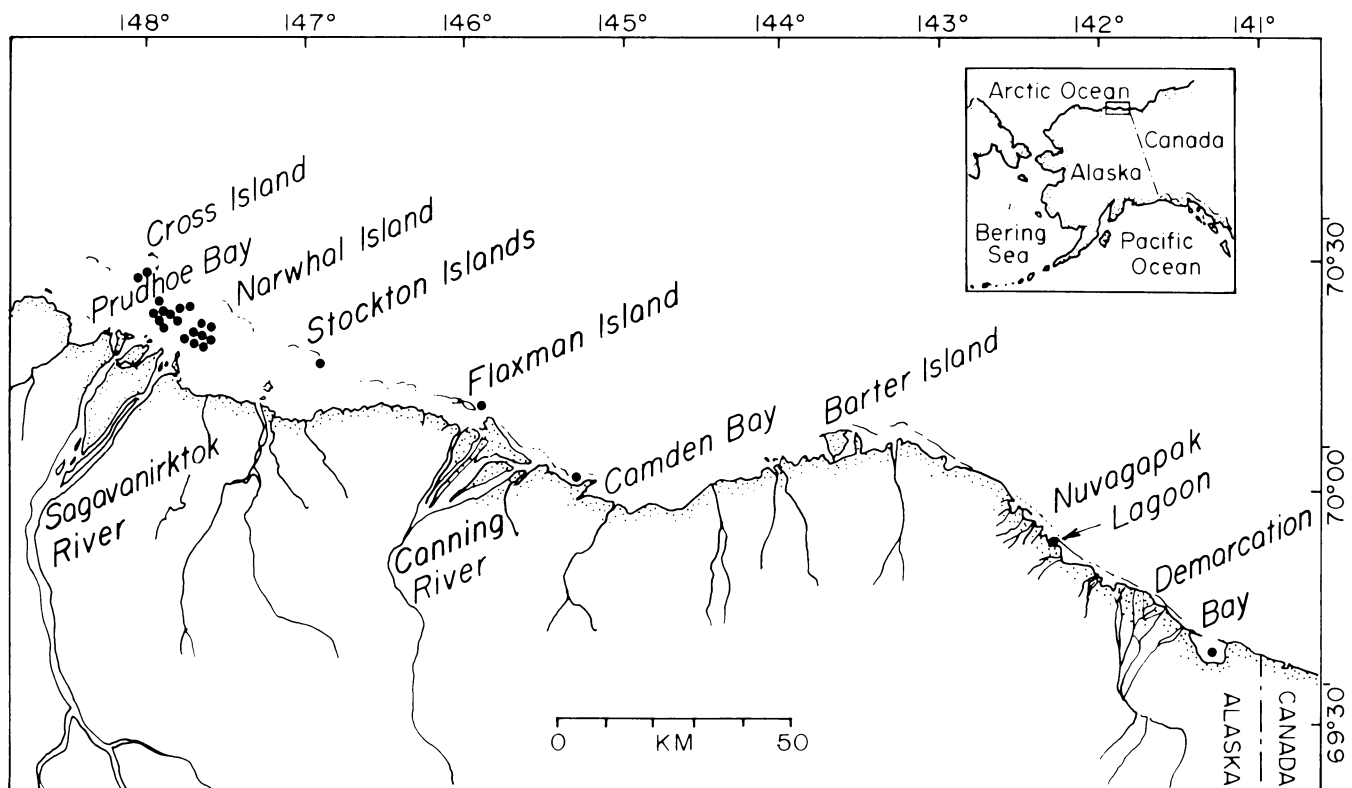

FIG. 5.   The eastern Alaskan Beaufort Sea shelf. Solid circles denote the location or suspected location of macroalgal beds based on biological or geological evidence.

vanirktok Delta (Fig. 1). In the left portion of this record, a thin layer of surface sediments overlies an indistinct and highly irregular, discontinuous sub-bottom reflector. At the point where other data (including side-scanning sonar and the Simrad record in particular) indicate that the Boulder Patch begins, a distinct sub-bottom reflector reaches the seafloor. Landward of this point, there are several seaward-dipping sub-bottom reflectors that are truncated by the seafloor, showing that the seafloor here is an erosional surface. Our diving traverses in different parts of the Boulder Patch show that there is only a thin layer of boulders, which is no more than one boulder thick. The 200 kHz bottom record, which showed boulders as spikes above the surrounding seafloor, indicates that the maximum height

of the boulders is about 70 cm. During our dives, we observed boulders of this height; horizontal dimensions were up to 2 m.

Existence of Other Macrophyte Beds in the Alaskan Beaufort Sea

Recently, other macrophyte beds have been located or are presumed present based on biological and geological evidence. The location of these beds in the Alaskan Beaufort Sea is shown in Figure 5. In two cases, algae were present in the absence of significant concentrations of rock substrata. However, none of the algal beds were large, not all contained kelp, and none possessed the diverse epilithic fauna that characterizes the Boulder Patch in Stefansson Sound.

Boulders and cobbles with attached kelp exist in a small area southeast of Belvedere Island in the Stockton Island chain, and northwest of Kangigivik Point in western Camden Bay (Barnes, 1981). Boulders and cobbles with attached kelp occur in a small area seaward of Flaxman Island at 10 m depth. In Nuvagapak Lagoon, kelp are absent but several species of red algae exist on a sandy-mud seafloor. Large *Laminaria saccharina* plants (1-3 m long) lie on a mud seafloor in Demarcation Bay. Their holdfasts are attached to clods of peat, clumps of tangled red algae, and detritus. Further offshore in the area north of Cross and Narwhal islands, cobbles and small boulders are numerous on the seabed at depths of 13-15 m. The establishment of macroalgae on these rocks is prevented by intensive ice gouging. However, the presence of kelp and red algae as drift on barrier islands and beaches along the entire Alaskan eastern Beaufort Sea coast suggests that at least scattered populations of benthic macroalgae exist on the nearshore shelf.

Sedimentation

Figure 6 shows the pattern of sedimentation at DS-11 between August 1978 and November 1981. Sedimentation was greatest in late summer and fall when 1-5 mm of sediment accumulated on the seafloor and biota. Storms in August and September created wave turbulence and wind-driven currents that suspended large amounts of sediment in the water column. These sediments remained suspended for long periods and settled slowly following freeze-up in October (Fig. 7). Intense storms were common just prior to or during freeze-up. Sedimentation decreased through the winter; less than 1.25 mm accumulated on the seafloor between mid-November and late February. Little or no sedimentation was documented between February and May, when we observed maximum water visibility

FIG. 7.   A thick layer of silt covers kelp plants, rocks and other biota in early November 1978, when the solid ice canopy is about 0.5 m thick. Particulate matter in the water column limits visibility to <1 m. The kelp blades are approximately 10 cm in width.

(greater than 20 m). One to two mm of sediment accumulated on the seafloor between May and late July. Water visibility in July and August ranged between 1 and 3 m, and continued to decrease through the summer and fall, until it reached a low of 0.5 m in early November.

Despite the periodic accumulation of sediments on the seafloor, observations made since 1971 indicate that the Boulder Patch is a nondepositional environment. Our observations over three years showed that sediments did not steadily accumulate on biota and boulders. We also have not noted the burial of hard substrata at other locations in the Boulder Patch.

Silt constituted the highest percentage (58.5%) of the material retrieved from the sediment collector between May and August, 1981. Clay (38.3%) and sand (3.2%) constituted the remaining fractions. The percentage of organic matter of the sediment was 8.4%.

Turbid Ice

In early November 1978, divers noted that the under-ice surface of the thin ice canopy was not flat and hard as expected, but was extremely irregular and soft. Much sediment was also entrapped in this ice canopy, leading divers to call it slush ice or turbid ice (Reimnitz and Dunton, 1979). The lower surface of the turbid ice had considerable relief (0.5 to 2.5 m; Fig. 8) and was capped by the solid ice canopy. The turbid ice was extremely porous and composed of large and small crystals of granular ice reaching 5 cm in length. If disturbed, even by diver's bubbles, sediment entrapped between the ice crystals would rain down to the seafloor, and the water near the disturbance would become turbid. We found that this turbid ice layer was slowly incorporated into the hard congelation ice as freezing advanced downward. Thus by late April, only the longest protrusions of of turbid ice were visible under the smooth ice canopy.

The distribution of turbid ice was widespread in the vicinity of the Boulder Patch. At DS-11, turbid ice has
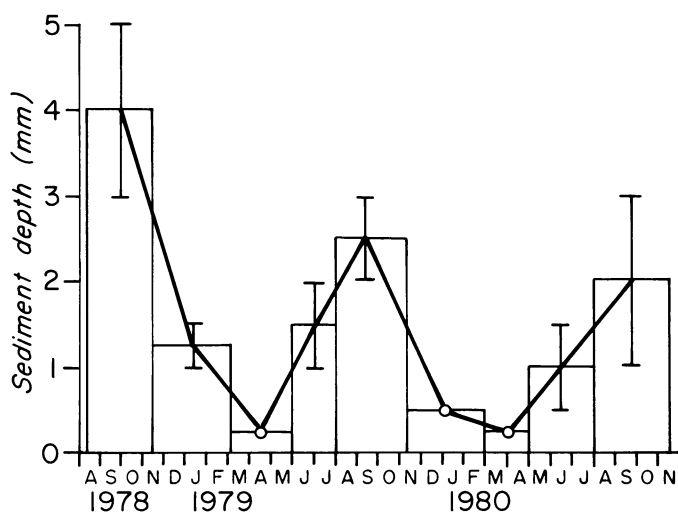

FIG. 6.   The pattern of sedimentation at DS-11, as measured seasonally on biota and anchored trays. Vertical bars represent ranges in sediment thickness. Open circles denote values below the limits of precise measurement (<0.5 mm).

FIG. 8. The irregular under-ice surface at DS-11, known as turbid ice. This ice formation contains sediments, is of variable thickness, and is soft. The organisms shown here attached to this ice layer are amphipods, and are 1.5 cm in length.

FIG. 9. Rock substrata are maximally utilized in the mature community by red crustose coralline algae, holdfasts of various species of red and brown algae, sponges (*Phakettia cribrosa*, right foreground), soft corals (*Gersemia rubiformis*, background), and other epilithic invertebrates. The sponges are ~10 cm in diameter.

been present every winter since 1978, except 1981. Due to the inclusion of fine sediments and particulates, light transmission into the water column was blocked completely, even during periods of 24-hour daylight. Photon flux density on the bottom at DS-11 in May 1979 under turbid ice was below the detection limits of our instrument. The spring bloom of ice microalgae, which is common in most arctic coastal areas (Alexander, 1974; Hsiao, 1980), did not occur in this area because of the total darkness. Thus, the presence of a turbid ice canopy restricted microalgal production to the short open-water period.

Fauna and Flora of the Boulder Patch

The Stefansson Sound Boulder Patch supports a well-established kelp community characterized by several species of red and brown algae, and by a diverse assortment of invertebrates respresenting every major taxonomic phylum. With the exception of rocks noticeably upheaved and overturned recently, nearly all exposed substrata are covered by algae and epilithic invertebrates (Fig. 9). Table 1 lists the predominant fauna and flora of the Boulder Patch, and provides data on density, biomass, and frequency of the various species. Many of these organisms were pre-

viously unreported from the Alaskan Beaufort Sea and are currently only known from the Boulder Patch. Animal species listed in Table 1 constitute about 86% of the faunal biomass based on the results of fifty 0.05-m² scrapes. Polychaete worms and representatives of other phyla (e.g., Foraminifera, Nemertea, Echinodermata) constitute the remaining 14%. We saw no obvious changes in the biomass or density of the flora or fauna over the three-year period of sampling.

The most conspicuous member of the community was the brown alga, *Laminaria solidungula*, whose distribution is primarily limited to arctic regions although it does occur as far south as Nova Scotia (A.R.O. Chapman, pers. comm.). Two other less common kelp species—*Laminaria saccharina* and *Alaria esculenta* — were also present; they and *L. solidungula* formed a brown algal overstory (Fig. 10). Beneath the kelp blades and in areas where kelp cover was sparse or absent, another floral assemblage dominates (Fig. 11). This community is typified by several species of foliose and terete forms of red algae. These species, in order of their biomass·m⁻², include *Phycodrys rubens, Phyllophora truncata, Neodilsea integra, Rhodomela confervoides* and *Odonthalia dentata. Ahnfeltia plicata* (a filiform red alga) was not collected in the scrapes, but it was present in the Boulder Patch. These red algal species and crustose corralines such as *Lithothamnium* were used by many invertebrates as a substratum for attachment.

This algal assemblage appears similar in species composition to algal assemblages found in the north Atlantic Ocean. Of the nine species of macroalgae, two are restricted to the Arctic Ocean, three are common to the Atlantic Ocean, and four are found both in the Atlantic and Pacific oceans. None has a distribution that is strictly Pacific. Lee (1973) noted in his review of Canadian macroalgae that the Canadian Arctic marine flora is distinctly temperate Atlantic in composition.

FIG. 10. The arctic kelp, *Laminaria solidungula*, constitutes the greatest percentage of the biomass in the Boulder Patch. In the center of the photograph is the crescent sponge, *Choanites lutkenii*, which is ~8 cm in width.

TABLE 1. Density ($N \cdot m^{-2}$), biomass ($g \cdot m^{-2}$) and frequency of occurrence (F) of the predominant benthic biota on rock substrata of the Boulder Patch

Species	$N \cdot m^{-2}$	$g \cdot m^{-2}$	F	Species	$N \cdot m^{-2}$	$g \cdot m^{-2}$	F
PORIFERA				**BIVALVIA**			
Choanites lutkenii		3.6	4	*Astarte* sp.	1.6	<0.1	6
Halichondria panicea		3.0	32	*Boreacola vadosa*	0.8	<0.1	4
Haliclona rufescens		2.5	44	*Musculus* sp.	239.6	0.1	82
Leucandra sp.		0.2	26	*Musculus discors*	69.2	2.1	8
Phakettia cribrosa		11.8	34	*Macoma calcarea*	0.4	<0.1	2
CNIDARIA				*Portlandia arctica*	0.4	<0.1	2
HYDROZOA				**BRYOZOA**			
Abietinaria sp.		<0.1	2	*Alcyonidium* sp.		1.0	44
Calicella syringa		0.1	30	*Callopora lineata*		2.6	90
Corymorpha sp.		<0.1	2	*Carbasea carbasea*		<0.1	2
Eudendrium sp.		<0.1	8	*Crisia* sp.		0.1	10
Lafoeina maxima		0.3	28	*Cyclostomata*		0.2	20
Obelia sp.		<0.1	12	*Dendrobeania* sp.		<0.1	2
Rathkea sp.		<0.1	2	*Eucratea loricata*		3.8	66
Sertularia cupressoides		8.5	86	*Flustra* sp.		0.1	2
Sertularia sp cf. *albimaris*		0.4	6	*Flustrella* sp.		<0.1	2
ANTHOZOA				*Hippothoa hyalina*		5.1	90
Gersemia rubiformis		3.0	14	**CHORDATA**			
MOLLUSCA				**ASCIDEACEA**			
GASTROPODA				*Chelyosoma macleayanum*	2.0	<0.1	8
Amauropsis purpurea	0.4	<0.1	2	*Mogula* sp. cf. *siphonalis*	0.4	0.4	2
Lacuna sp.	0.4	<0.1	2	*Mogula griffithsii*	1.2	0.3	8
Margarites sp.	2.4	<0.1	10	*Styela rustica*	0.4	<0.1	2
Margarites costalis	1.6	<0.1	2	**OSTEICHTHYES**			
Oenopota sp.	1.6	<0.1	6	*Liparis herschelinus*	0.4	0.1	2
Plicifusus sp.	1.2	<0.1	2	*Myoxocephalus quadricornis*	0.4	2.9	2
Polinices sp.	0.8	<0.1	2	**PHAEOPHYTA**			
Retusa obtusa	1.2	<0.1	2	Laminariales			
Solariella sp.	2.0	<0.1	6	(10-25% rock cover)[1]		66.7	20
Solariella varicosa	0.8	0.1	4	Laminariales			
POLYPLACOPHORA				(>25% rock cover)[1]		262.1	54
Amicula vestita	16.0	11.0	38	**RHODOPHYTA**			
Ischnochiton albus	1.2	<0.1	2	Crustose corallines		0.5	20
				Neodilsea integra		30.9	26
				Odonthalia dentata		4.2	40
				Phycodrys rubens		45.3	88
				Phyllophora truncata		33.4	80
				Rhodomela confervoides		5.3	58

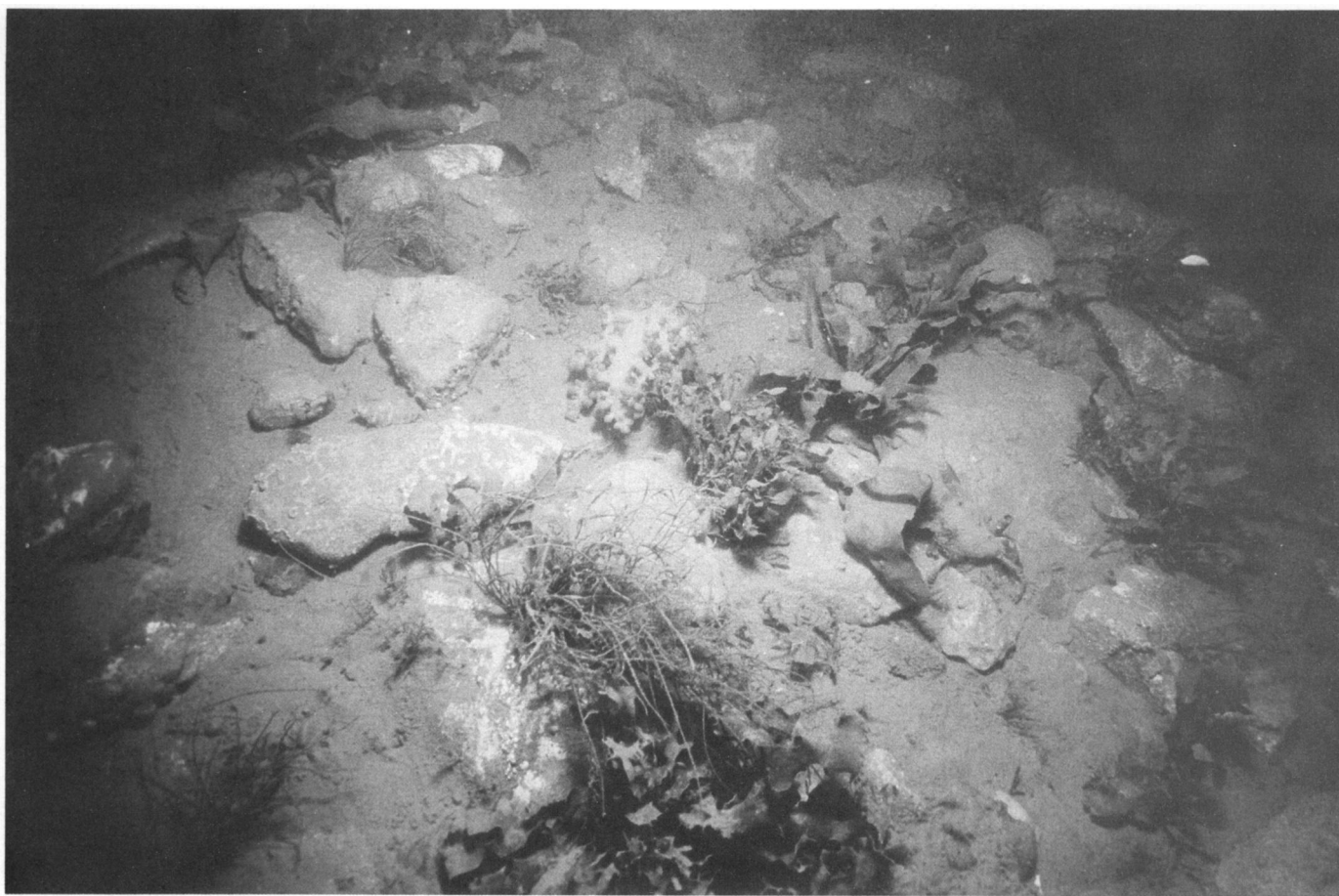[1]Includes *Laminaria solidungula, L. saccharina* and *Alaria esculenta.*

FIG. 11. Beneath kelp blades or in areas where kelp is absent, several species of red algae are found attached to rocks. The terete-branched alga in center foreground is *Rhodomela confervoides* and the large-bladed red alga in the right center is *Neodilsea integra*. Adjacent to the soft coral in the center, *Phycodrys rubens* is attached to *Phyllophora truncata*. White patches on rocks are remnants of dead crustose corallines. Live crustose corallines cover most exposed rock surfaces in this photograph. The soft coral is ~8 cm in length.

Sponges and cnidarians are the most conspicuous invertebrates. This is due to the large size of some species, their abundance, and their striking shapes and colors. Two sponges — *Choanites lutkenii* (Fig. 10) and *Phakettia cribrosa* (Fig. 9) — and the delicate pink soft coral *Gersemia rubiformis* (Fig. 9) are widespread. All three species are represented by individuals of all size classes. At least four sea anenomes (order Actinaria) are present, but their identities remain uncertain at this time. Other conspicuous invertebrates include several species of *Tubularia*, a stalked hydrozoan. Smaller less-conspicuous epilithic animals (such as hydroids and encrusting sponges) form a turf-like covering on rocks. They are associated with *Rhodomela confervoides* (a terete-branched red alga) and stringy masses of the red alga, *Phycodrys rubens*.

Molluscs, bryozoans, and members of the urochordate group are common on rocks and attached to other biota, but are less conspicuous than the cnidarians and sponges. The chiton *Amicula vestita* constitutes the greatest percentage of molluscan biomass, and juvenile mussels of the genus *Musculus* have the greatest density. *Amicula* is an active herbivore; it feeds primarily on the blade and stipes of *Laminaria solidungula*. Erect and encrusting colonies of

bryozoans are common on rocks and red algae. Colonies are often associated with hydroids and the translucent ascidian, *Mogula griffithsii*. The inconspicuous sea spider, *Nymphon grossipes* (not listed), is usually found among these dense mats of algae and attached invertebrates.

Several species of bottom-dwelling fishes are present in the Boulder Patch. Only two — the clingfish *Liparis herschelinus* and the four-horned sculpin *Myoxocephalus quadricornis* were collected in scrapes. The other species include the eelpout *Gymnelis viridis* and juvenile *Liparis* sp. In March of 1979 and 1980, thousands of small eggs were found attached to kelp stipes, wire flags, and anchor lines. Large numbers of tiny liparid-like fishes were also observed, suggesting that these eggs were laid by adult *Liparis* females in the preceding months.

A majority of the species collected, but not listed in Table 1, are those found in the annelid, arthropod, and echinoderm groups. Over 100 species of annelids and arthropods were found in the Boulder Patch, and many of them are found throughout the Arctic. Those annelids and arthropods uncommon on soft bottoms but common in the Boulder Patch include the tubicolous polychaetes *Spirorbis* spp., the fanworm *Potamilla neglecta*, and the barnacle *Balanus*
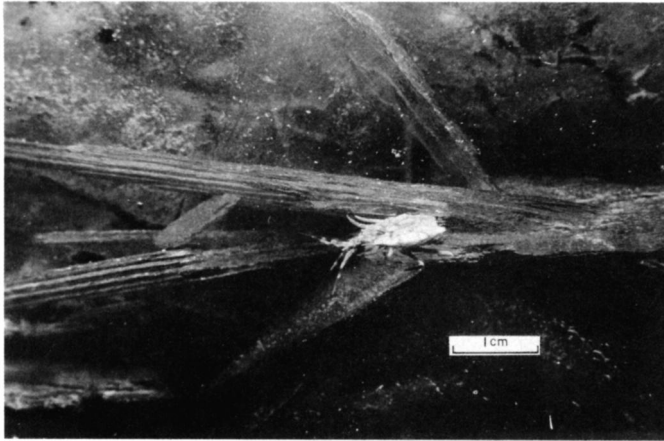
FIG. 12. The amphipod *Gammaracanthus loricatus* is commonly found clinging to large ice platelets in the turbid ice canopy. Sediment can be seen on the horizontal and vertical surfaces of these ice platelets, which here are ~7 cm in diameter.

TABLE 2. Organisms found in the turbid ice canopy and their reproductive condition

Organism	Reproductive State
INVERTEBRATA	
POLYCHAETA	
Antinoella sarsi	gravid
AMPHIPODA	
Gammaracanthus loricatus	gravid
Gammarus setosus	
Melita formosa	gravid
Onisimus litoralis	
Weyprechtia pinguis	
VERTEBRATA	
OSTEICHTHYES	
Boreogadus saida	

sp. *Spirorbis* forms small (1-4 mm) spiraled tubes attached to rocks, algae, hydroids and snail shells. *Potamilla*, a much larger polychaete, was found attached to rocks and algae, and had membranous tubes 8 cm or longer. The small barnacle *Balanus* was also observed frequently but was never seen in clusters of more than three individuals.

The largest motile invertebrate was the crustacean *Hyas coarctatus alutaceus*. We frequently found this animal and the hermit crab *Pagurus trigonocheirus* in thick kelp, but they were rare where kelp cover was sparse. Small motile crustaceans common to the Boulder Patch were mysids, amphipods, and (to a lesser extent) isopods. Other motile invertebrates included five-rayed and six-rayed seastars, *Leptasterias* spp. and the 10-rayed sunstar, *Crossaster papposus*.

Several species of marine organisms appear to be associated with the presence of the turbid ice canopy (Table 2). Gravid amphipods and polychaete worms were commonly observed between ice platelets or clinging to large ice crystals (Fig. 12). Arctic cod were seen swimming along the ice formations. We collected several types of benthic biota from this ice canopy, including red algae, *Laminaria*, bryozoans, bivalves, and hydroids. These benthic organisms eventually disappear as they become incorporated into the ice canopy but the motile organisms are present throughout the winter.

Recolonization

The results of the recolonization experiment are presented in Table 3. Recolonization of the denuded plots was a slow process and was still incomplete after three years. At least 50% of the substratum remained bare on all plots; on most plots, over 75% of the substratum was uncolonized. Of the 14 denuded plots, 11 showed the establishment of some type of animal or plant assemblage, one remained bare, and two (numbers 10 and 12) were dropped from the experiment due to inadequate photographic documenta-

tion of the recolonization process. Recolonization by algae and hydroid colonies was quantified by estimating percent cover, and density was used to document the establishment of *Spirorbis* worms and one unidentified animal. The recolonization of the 11 plots was characterized by the appearance of either crustose coralline algae, *Neodilsea integra*, hydroids, *Spirorbis*, or by a red circular encrusting organism called Unknown Species A. This species is very small, 1-2 mm in diameter, and is impossible to identify from photographs.

The photographs showed that encrusting coralline algae were seldom entirely removed from the rock substratum, regardless of our scraping efforts. Therefore, in Table 3, we present data on the recovery of crustose corallines in plots where they existed previously. In no case were encrusting coralline algae observed to colonize a completely bare substratum. *Spirorbis* colonized the most plots. Hydroids and *Neodilsea* were found on only three plots by November 1981. In some cases, the hydroid cover appeared to decrease between successive field seasons. The time of denuding did not appear to have any effect on the appearance of the plots after a three-year period. We did note that *Spirorbis* settlement took place between March and May and Unknown Species A settled between February and August. But these two species did not colonize the rock surfaces within the first 12 months following denuding.

Most plots contained an assemblage of biota within nine months of denuding. Many of the colonizing organisms first appeared in the early winter months. This may be due to the lack of sediment covering the plots at that time. The sediment cover is substantial in the summer and fall, and small organisms — if they exist — cannot be observed. Motile invertebrates (primarily chitons, snails, seastars and polychaetes) were frequently observed on the plots.

TABLE 3. The density and percent cover of organisms observed in November 1981, on plots denuded in 1978 and 1979

Plot Number	Date Denuded	Crustose Corallines % cover		Neodilsea % cover	Hydroids % cover	Spirorbis density	Unknown Species A density
		Start	Final				
1	8/78	12	25	2			
2	8/78	25	35		2		
3	8/78	5	10	5		4	
4	11/78	1	3				
5	11/78	8	10	30	1	1	
6	11/78	5	8				
7	11/78	8	10		3		
8	3/79					5	3
9	3/79					2	3
11	3/79	Colonization not sufficient to quantify					
13	5/79			1		2	
14	5/79					10	

FIG. 13. The pattern of blade growth (means ± 95% confidence limits) in *Laminaria solidungula* in relation to seasonal variation in inorganic nitrogen concentrations.

These animals were observed in more than 15% of the plot photographs taken over the study period. But we found it impossible to determine whether these animals were actively feeding or merely traversing the substratum in search of food. Many of the seastars we observed on the plots were in a pinwheel configuration, brooding eggs, and obviously not feeding.

Linear Growth and Productivity of Laminaria solidungula

Laminaria solidungula is attached to the substratum with a discoidal holdfast that gives rise to a stipe of variable length and a blade that is divided by constrictions into one to four ovate segments of different sizes. Our initial studies found that the constrictions formed in late November, followed by the appearance of a new ovate segment by the following February. We observed this pattern of growth for over three consecutive years and have confirmed that the length of each ovate segment corresponds to one year's growth.

Figure 13 shows the results of growth measurements taken from August 1978 to November 1980. The lowest rate of linear growth occurred during the ice-free periods (from July to November), and the growth averaged 0.16-0.25 mm per day. The growth rates increased in fall and reached an average maximum of 1.14-1.41 mm per day in late winter or early spring. We may not have measured peak growth during the 1978-1979 winter season because of the timing of the visit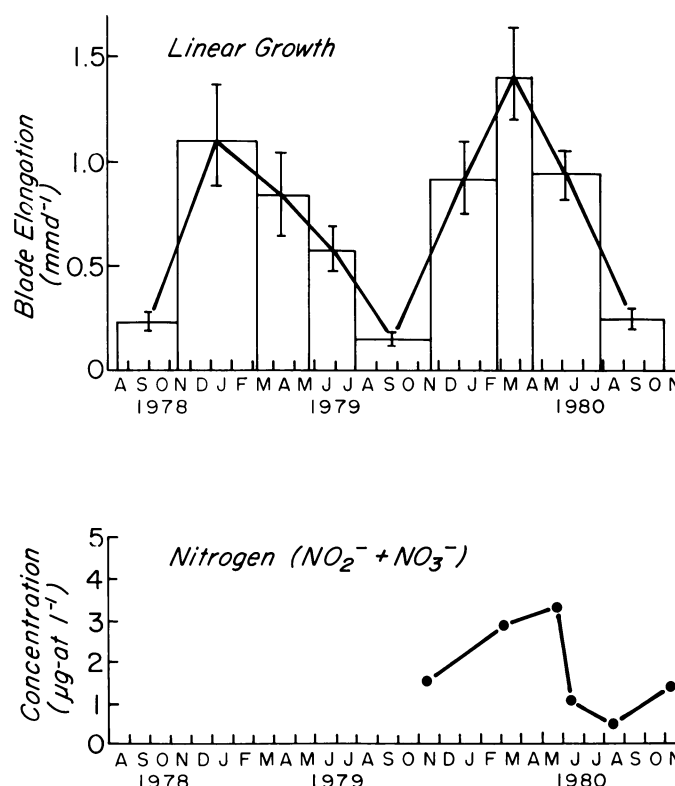s to the study site. Growth rates decreased during spring and early summer. Since the turbid ice canopy in Stefansson Sound prevented penetration of light between October and early July, these plants completed almost all of their annual linear growth in absolute darkness.

Levels of inorganic nitrogen in the form of NO_2^- and NO_3^- in the seawater are shown beneath the growth curves in Figure 13. The concentrations of inorganic nitrogen follow an annual cycle typical of arctic (Chapman and Lindley, 1980) and temperate waters (Chapman and Craigie, 1977; Wheeler and North, 1980). In November 1979, the level of inorganic-N was 1.5 microgram-atoms·liter^{-1} (μg-at·l^{-1}) and it increased to 3.3 μg-at·l^{-1} in late May before decreasing to less than 0.1μg-at ·l^{-1} in August. By November 1980, the concentration had increased to a level similar to that of the previous November (1.2 μg-at ·l^{-1}). The winter growth of *L. solidungula* occurs during higher concentrations of inorganic nitrogen. A similar relationship between growth and nitrogen availability was also observed for *L. solidungula* in the Canadian High Arctic by Chapman and Lindley (1980).

Figure 14 shows the annual net increase in biomass of 17 plants as a function of their initial weight. The average annual production-to-biomass ratio (P:B) was 0.95 ± 0.14 (mean ± 95% confidence limit), and the annual mean growth was 0.0022 g·g^{-1}·d^{-1} (grams of wet weight added per gram of plant per day). The standing crop of all three species of kelp (of which *L. solidungula* constituted over 95%) ranged from 67 g·m^{-2} in areas of 10-25% rock cover to 262 g·m^{-2}
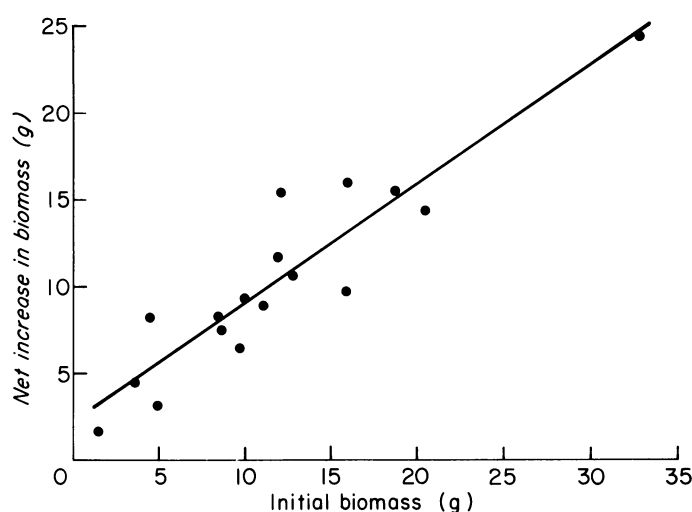
FIG. 14. Annual net increase in biomass as a function of initial biomass in *Laminaria solidungula* plants living under a turbid ice canopy; correlation coefficient, 0.92.
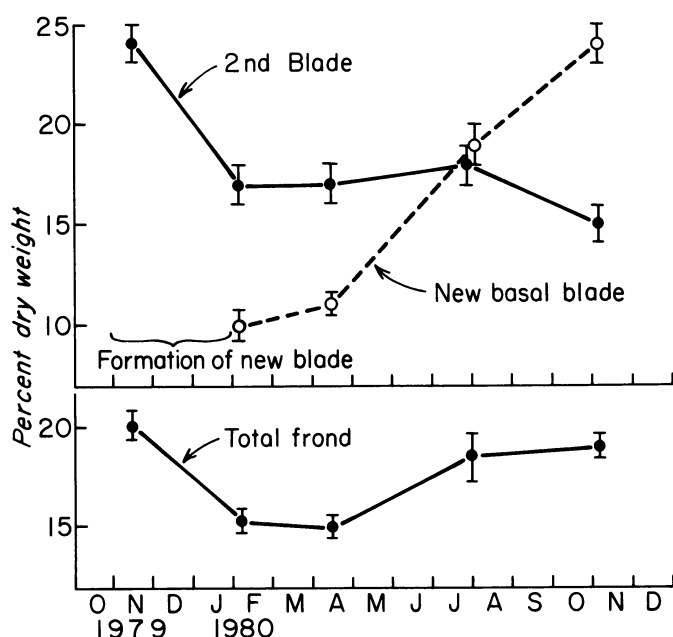

FIG. 15. Seasonal variation in percent dry weight of wet weight in the entire blade (or frond), and in the basal and second blade segments of *L. solidungula* plants. All means ± 95% confidence limits.

where rock cover exceeds 25%. Using the results of the geophysical surveys conducted by Toimil (1980), the area of 10-25% rock cover is about 13 x 10^6 m^2, and the area with cover >25% is 7.3 x 10^6 m^2. Integrated over these areas, the standing crop of the kelp is estimated to be 2.8 x 10^9 g.

The changes in percentage dry weight to wet weight of several plants (N = 15 to 25) and their blades are shown in Figure 15. The highest percentage dry weight of the entire blade occurred in November, decreased between November and May, and increased from May to previous November levels. The percentage dry weight of the second segment

(the growth increment of the previous season) and the developing first (basal) blade segment varied inversely to each other. Between November and February, the percentage dry weight of the second segment dropped from 24 to 17%, which concurred with the formation of a new basal segment. The percentage dry weight of the new basal segment increased steadily from 10% in late February to 24% by November, when a new basal segment again began to develop. The second segment did not retain its original dry weight percentage, but dropped to 15% by early November. The percentage dry weight of blade segments distal to the second segment and the stipe (data not shown) varied little throughout the year. Percentage dry weight of the segments distal to the second blade were highest in summer, and ranged annually between 14 and 18%. The percentage dry weight of the stipe varied between 23 and 25%.

DISCUSSION

The Origin and Modern Physical Processes of the Boulder Patch

Deposits of gravel, cobbles and boulders similar to those found in the Boulder Patch of Stefansson Sound are being formed today in a number of places during the erosion of coastal bluffs containing coarse materials. Such stones are found in parts of the Quaternary Gubik Formation, which blankets much of the coastal plain (Black, 1964). Leffingwell (1919) first drew attention to the boulders occurring in large numbers along the beaches of Flaxman Island, and called them the Flaxman Formation. The Flaxman boulders have since been studied in other areas by MacCarthy (1958), Rodeick (1975), and Hopkins (1979). According to these studies, the rocks include many types clearly extrinsic to northern Alaska. Among them are rea granite, granulite-facies metamorphic rocks, pyroxenite, diabase, pink quartzite, and dolomite. The origin, mode of transport and emplacement of these erratics are under debate. One theory proposes that the rocks were rafted by ice to northern Alaska during times of relatively higher sea level (Hopkins, 1979). A second theory suggests that the boulders and cobbles were transported via a continental ice sheet (A.S. Naidu, pers. comm.). The sources of rocks whose mineralogy matches those in the Boulder Patch are northern Greenland for ice-rafted erratics, and the Canadian Shield for rocks transported via a continental ice sheet.

Studies of sections of the Gubik Formation exposed on land, and of offshore borings (including several from Stefansson Sound; Harding-Lawson Associates, 1979), identify the layer containing cobbles and boulders as a thin sheet of glaciomarine stony sandy silt (Hopkins, 1979). The layer overlies marine clays deposited during the last major interglacial transgression, and — according to Hopkins — it may mark a local transgression resulting from the weight of ice over arctic Canada during early Wisconsinan

Age. This Flaxman Formation is older than 42 800 years (Hopkins, 1979).

Bluffs along the Beaufort Sea shores usually retreat 1-3 m·yr⁻¹ (Owens et al., 1980). Wherever the eroded materials contain glacial dropstones from the Flaxman Formation, the fine materials are winnowed out by waves and currents, and the cobbles and boulders are left behind. The cobbles and boulders left behind on the beach are known as lag deposits. In many nearshore areas, these lag deposits rest on consolidated mud, and they are common on the beaches of Stefansson Sound (Fig. 3). During continuing coastal retreat, the cobbles and boulders are left behind and may eventually be buried by shallow marine sediments, as pointed out by Reimnitz and Ross (1979). Coastal bluffs west of Stefansson Sound rarely contain boulders.

All evidence suggests that the modern littoral boulder lag deposits are separated from the Boulder Patch by a wide belt of surficial shallow marine deposits as shown in Figure 4. Since the boulders in many areas of the Boulder Patch are resting directly on consolidated mud (similar to numerous places on shore) one is tempted to connect the coastal boulder lag deposits with the Boulder Patch, but we have no evidence to support this (Reimnitz and Ross, 1979). Thus the Boulder Patch apears to be an isolated area.

The seismic reflection records in many regions of the Boulder Patch show "windows" in the Holocene marine sediment cover where boulders are found on the sea floor. These windows are considered an erosional surface. Diving observations indicate that the cobbles and boulders generally rest loosely on top of a firm mud substratum, and are not enclosed by the substratum. Thus the Boulder Patch is a lag deposit presently resting on older marine mud, while the formerly overlying Flaxman Formation has been eroded away. This erosion may have occurred during lower sea level stands of the Holocene transgression (Reimnitz and Ross, 1979). Our observations provide evidence that the erosion is an ongoing process.

Reimnitz et al. (1979) discussed the enigma of the apparent lack of arctic delta accretion, and the existence of the Boulder Patch instead of deltaic deposits of the Sagavanirktok River. Midsummer measurements at DS-11 (made shortly after peak discharge of the nearby Sagavanirktok River) showed only small amounts of suspended sediment accretion, while the largest slugs of suspended sediment were collected in fall, when river discharge is low (Fig. 7). By February, sediment cover on plants and rocks was reduced to a barely measurable film of ooze. Matthews (1981b) recorded under-ice currents decreasing from 1.4 to 0.7 cm·s⁻¹ during the period between November and December at DS-11. Peak velocities during this time barely exceeded 9 cm·s⁻¹. By late January, maximum velocities were less than the threshold of the instrument (about 2 cm·s⁻¹). The fact that the major seasonal sediment accumulations at DS-11 were being swept away by currents of <10 cm·s⁻¹ suggests that the sediments had been deposited after, not

during, the major fall storms when currents are strong. The major fall events, during which the large volumes of resuspended bottom sediments are entrained into a thick turbid ice layer (Reimnitz and Dunton, 1979; Barnes et al., 1982), were not recorded by our sedimentation measurements. The turbid ice above DS-11 contained coarse shell fragments and pebbles up to 2 cm in diameter. These particles could be rafted several tens of kilometers during ice breakup. Summer sediments settling from suspension into the trap at DS-11 contain 97% silt and clay-size materials, and 3% sand. Barnes et al. (1977) recorded summer currents in Stefansson Sound "strong enough to erode and transport medium to fine sand." Thus there is not only suspended sediment transport, but also bedload transport, mainly westward through the Boulder Patch. Observations on stakes driven into consolidated mud, and repeated photography of a cobble with an attached kelp in Stefansson Sound also demonstrated slight erosion within a period of only several months (Toimil and England, 1982).

A hard rock substratum is one requirement for the growth of macroalgae, and is provided by the presence of boulders, cobbles, and pebbles on the floor of Stefansson Sound. Another requirement is that this substratum be cleaned periodically of fine sediments that accumulate seasonally, since these sediments would eventually smother the community. Waves and currents provide such cleaning. Cleaning may also result from the erosive action of frazil ice formed during fall storms, and from the subsequent ice rafting of entrained sediment. Still another requirement is protection from deep draft multiyear ice which has the potential to physically disrupt and overturn bottom materials at frequent intervals (Reimnitz et al., 1977; Barnes et al., 1978). This requirement is satisfied by a chain of protecting barrier islands that greatly reduce the flux of pack ice and allow the establishment of a floating fast-ice canopy in winter. Understanding these requirements will aid in the search for other kelp beds in the Beaufort Sea.

The scattered occurrences of kelp beds found in our reconnaissance surveys of the Beaufort Sea largely satisfy the above requirements. All but the Demarcation Bay occurrence are found in association with boulders and cobbles of the Flaxman Formation, and all are in areas of minimum sedimentation. The occurrences lie either in partial protection of islands, or in the protection of grounded ice which plays the role of offshore islands in the stamukhi zone (Reimnitz et al., 1978). However, off the major coastal promontories (where westward moving pack ice interacts with the continent), frequent ice-bottom interaction precludes the establishment of kelp on cobbles. The stamukhi zone closely skirts Narwhal and Cross islands, where pebbles and cobbles are abundant on the sea floor but bare of growth.

The number of boulders and cobbles increases eastward of Stefansson Sound toward the Canadian border, and so does the amount of surficial gravel, as seen in recent reconnaissance surveys east of Barter Island. But to date,

we suspect no other major occurrences on the Alaskan Beaufort Sea shelf. A semi-elliptical region of sandy gravels, sands and consolidated pebbly mud exists on the shelf east of the Canadian border. Yorath *et al.* (1970) tentatively identified these as relict glacial deposits and ice-pressed tills. The shallowest portions of this area are free of modern sediment and relatively protected by Herschel Island against the westward-moving pack. These shallows seem to be suitable for the growth of macroalgae. This region may be the source for much of the algal remains washed up on the beaches east of Camden Bay.

Physical Processes and Community Development

The results of our recolonization studies show that development of an epilithic assemblage or oganisms is a slow process in the Arctic compared to temperate latitudes. This is in part a result of the total absence of ephemeral species. Recolonization experiments in temperate kelp beds show that a diverse and dense assemblage of biota is established within one year (Foster, 1975). Only a sparsely established assemblage was seen after three years in Stefansson Sound. The factors influencing establishment of an epilithic community on the boulders denuded in the Boulder Patch include the stability of the substratum, temporal variability in the composition and abundance of larvae and spores, biological interactions such as predation, herbivory, and competition, and the growth rates of the species that settle. These factors have been identified as important in the establishment and development of communities in temperate regions by Dayton (1971), Foster (1975), Dunton (1977) and Osman (1977).

A completely different pattern of establishment and development compared to that on natural substratum was noted on styrofoam floats used to mark the different experimental plots. These small square floats (100 cm^2) were suspended 1 m above the seafloor at different seasons. They were not examined quantitatively since they were never intended as experimental substrates. However, they provided interesting comparative data on the process of recolonization in the Boulder Patch. The floats were smaller than the experimental plots and remained relatively free of sediments. Furthermore, the floats were not subject to grazing or predation pressures by benthic animals.

The floats were first examined about 12 months after initial deployment. At that time, all were covered with hydroids, bryozoans, red algae and polychaete worm tubes. The early establishment of these colonizers on the suspended floats suggests that the absence of spores and larvae in the water column is not a factor responsible for the limited colonization of denuded boulders. Growth of species identical or similar to those on suspended floats also appears to be slower on the denuded plots. Although larvae and spores may be exhibiting a substratum preference for styrofoam, it is not likely that all epilithic species would possess a common selectivity for an artificial substratum. Instead, we believe other factors must be involved; i.e.,

FIG. 16.   Sediment cover on a recolonization plot is made apparent by the trail left by the chiton *Amicula vestita* (top right center). Other smaller trails in the sediment cover were made by polychaete worms. A small tubeworm, *Spirorbis* (marked with an arrow), is the only organism that has colonized this plot since it was denuded 17 months earlier. Photo taken 29 July 1980.

either colonization is being prevented by sedimentation or an efficient predator or grazer is removing the organisms from the rock substratum.

The possible significance of these two factors in the recolonization process is exemplified in Fig. 16. Periodic sedimentation and the existence of active grazers and predators may act together in inhibiting settlement and in regulating development of opportunistic species. Competition is probably not important, as suggested by the abundance of free space on the plots after three years and the limited contact among colonizing species. This is in contrast to the total utilization of rock space in the mature community. Our observations indicate that sedimentation is a periodic physical disturbance that inhibits successful settlement by larvae and spores. In addition, potential grazing and predation pressures may interfere substantially with subsequent growth and development of the species that become established.

The periodic inundation by sediment in the Boulder Patch may adversely affect the process of recolonization by effectively blocking larvae or spores from reaching the rock surface, or by smothering epilithic biota with a stature of less than 1 or 2 mm (Fig. 16). The availability of primary substratum for recolonization is thus substantially limited during periods of sedimentation. Provision of primary substratum in the Boulder Patch is dependent on physical processes to remove sediment and disturb the cobbles and boulders.

New primary rock surfaces are exposed by water currents and ice gouging. Biological interactions do not appear to prevent the monopolization of space in the Boulder

Patch by a benthic organism (such as by crustose corallines) as has been shown in intertidal communities (Dayton, 1971; Menge, 1976; Grant, 1977). Ice gouging, although infrequent, is the only mechanism by which large cobbles and boulders are displaced. The factors that determine the frequency by which small cobbles are overturned are: current velocity resistance caused by large epilithic organisms (kelp, soft corals, and sponges) attached to the rock; and the size of the rock. The existence of white calcified deposits of crustose corallines covering the underside of many small cobbles in the Boulder Patch suggests that this process is a common event, and we have documented the overturn by strong currents of rocks with attached biota. The displacement of rocks by currents appears to be one of the most effective mechanisms that supplies substrata free of crustose corallines for recolonization.

The Importance of Turbid Ice to Invertebrate Fauna

Turbid ice is peculiar to high-latitude environments and significantly affects the biological environment of the Boulder Patch. It effectively restricts primary productivity to the summer open-water months and provides a substratum for a large population of motile invertebrate animals. Although common in Stefansson Sound, turbid ice is not common offshore. Outside of Stefansson Sound, its distribution along nearshore areas of the Alaskan Arctic coast is poorly known.

The animals commonly associated with the turbid ice canopy include five species of amphipods and one species of polychaete worm. None of these animals were observed feeding. This observation is supported by gut analysis of animals collected throughout the winter.

Laboratory analyses of these animals also revealed that they contained large amounts of yellow oil droplets. These large droplets are visible without magnification through the organism's exoskeleton. MacGinitie (1955) also noted the storage of oil in shrimp, copepods, and amphipods in the Arctic, and suggested that this stored oil is used in winter as a food reserve or for the production of gametes. Our observations also support this hypothesis.

Growth and Productivity of Laminaria solidungula and Its Importance to the Community

The pattern of growth in *Laminaria solidungula* corresponds closely to that of perennial kelps examined in other north temperate and arctic regions. The results of these studies demonstrate that seasonal growth is strongly correlated with the availability of inorganic-N in both *L. longicruris* off Nova Scotia (Chapman and Craigie, 1977) and *L. solidungula* in the Canadian High Arctic (Chapman and Lindley, 1980). The ability of these plants to store carbohydrate reserves in the form of laminarin or mannitol has also been shown, but the utilization of these reserves is probably limited to short periods when photosynthesis does not entirely support the carbon demand of blade elongation (Hatcher *et al.* 1977; Chapman and Lindley, 1980). In

contrast, our findings show complete dependence by *L. solidungula* on stored carbohydrate reserves to complete nearly all of its annual linear growth over long periods of complete darkness.

In *L. solidungula,* as in other *Laminaria* species, variation in percentage dry weight follows laminarin variation closely (Black, 1950; Chapman and Lindley, 1980), reflecting the amount of carbohydrate stored in the blade. Carbon fixed during the previous summer (and stored in what becomes the second distal blade segment) provides the carbon needed for the basal segment, as evidenced by a 7% drop in tissue density in the second segment between November and February. Growth of the new basal segment may also be supplemented to a small degree by carbon translocation from portions of the plant distal to the second segment. The ability to translocate photosynthetic products is characteristic of the kelp order Laminariales (Schmitz and Lobban, 1976) and appears to be characteristic of *L. solidungula.* The dependence of *L. solidungula* on stored food reserves reflects the functional significance of carbohydrate storage in these plants. A similar function has been documented in *Laminaria hyperborea,* which grows on the west coast of Europe. Luning (1971) found that *L. hyperborea* relied heavily on stored reserves for growth between October and March, when irradiance was below the compensation point. In another study he found that plants can produce a small new blade during their first half year in complete darkness (Luning, 1969). In contrast to both *L. solidungula* and *L. hyperborea,* the carbohydrate reserve in *L. longicruris* is exhausted before the onset of winter growth (Chapman and Craigie, 1978). The ability to store the products of photosynthesis thus appears best developed in plants periodically exposed to prolonged periods of low light.

Growth in *L. solidungula* in the Boulder Patch is both energy- and nitrogen-limited, since the two resources are not available in sufficient quantities simultaneously. During the summer open-water period when light is available, the plants must fix all the carbon necessary for their annual growth, reproduction, and metabolism. Little growth occurs during this period due to insufficient concentrations of inorganic-N needed for the synthesis of new tissue. Instead, the products of photosynthesis are stored and used during the winter when inorganic-N is available for the production of a new blade. Inorganic-N is depleted as a result of the annual spring bloom of microalgae and is slowly replenished through regeneration and exchange with ocean water. Our *in situ* growth studies of *L. solidungula* show that these plants can produce 95% of their original biomass as new plant tissue annually. Based on this, the net carbon contribution made by these plants to the ecosystem can be calculated from data on standing crop and carbon content.

The standing crop of kelp in Stefansson Sound is is 0.48×10^9 g dry weight assuming that the standing crop of 2.8×10^9 g is about 17% dry matter (Fig. 15). Over 90% of the standing crop is *L. solidungula.* The carbon content of

the dry matter in *L. solidungula* is approximately 31% (Chapman and Lindley, 1981) and varies little seasonally. On this basis, the annual energetic contribution made by the kelp in Stefansson Sound is 146 x 10^6 g C or about 7.2 g C·m^{-2} based on a P:B ratio of 0.95. This estimate does not take into account any patchiness in the turbid ice canopy or its complete absence in some years.

Using similar techniques at the same latitude in the Canadian High Arctic, Chapman and Lindley (1980, 1981) calculated the productivity of *L. solidungula* to be about 20 g C·m^{-2}·yr^{-1}. Linear growth was nearly 60% greater than in the Alaskan plants. The apparent lower productivity of the Boulder Patch community compared to the Canadian kelp bed is due to two factors: the absence of winter photosynthesis in Alaskan plants and a lower standing crop. Beneath patches of clean, transparent ice near DS-11, annual linear growth of kelp increases by 35% (Dunton and Schonberg, 1980). We attribute this growth to winter photosynthesis. In the Canadian kelp bed, the mean standing crop was ~870 g·m^{-2} (Chapman and Lindley, 1981), whereas the standing crop in the Boulder Patch ranged from ~70-260 g·m^{-2}. The difference in standing crop alone could account for the higher productivity recorded in the Canadian High Arctic.

Our estimate of carbon production does not include the carbon released as dissolved organic matter. This may occur during the summer, when there is an assimilatory surplus, or in early winter when meiospores are released. The release of dissolved organics by kelp may be 25-40% of gross production based on recent studies (Khailov and Burlakova, 1969; Hatcher *et al.*, 1977; Newell *et al.*, 1982). The carbon contribution by kelp in the Stefansson Sound Boulder Patch appears to be roughly equivalent to the contribution made by phytoplankton, which ranges from 5 to 20 g·m^{-2}·yr^{-1} at this latitude (Apollonio, 1980; Schell *et al.*, 1982). However, it is much lower than kelp production at more temperate latitudes (e.g., a *L. longicruris* community in Nova Scotia ranged between 143 and 428 g C·m^{-2}·yr^{-1}; Hatcher *et al.*, 1977).

The role of kelp as a carbon source in the marine environment is not well understood. Our observations show that few organisms feed directly on kelp in the Boulder Patch. Herbivores include only chitons and snails. We suspect, however, that other organisms derive nutrition from this abundant and ever-present carbon source. Over 90% of the carbon produced by macroalgae is thought to enter detritus food chains in either dissolved or particulate form (Mann, 1975). But tracking the path of kelp carbon through a detrital food chain is difficult using conventional biological methods. Current studies using natural carbon isotope ratios may determine the importance of kelp as a source of carbon for the biota of the Boulder Patch (Dunton and Schell, 1982).

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